TORREYA

Vol. 43 DECEMBER 1943 No. 2

Viruses in Relation to the Growth of Plants*

L. O. KUNKEL

About twenty-four years ago, Nishimura (10) reported that *Physalis alkekengi* allowed the tobacco mosaic virus to multiply within its tissues but showed no symptoms of disease. Since that time other masked carriers of plant viruses have been studied (2, 3, 9). We now know that practically all potatoes produced in this country carry the X virus but that, unless it occurs in combination with some other potato virus, no well defined symptoms are produced (3). We also know that some of the mutants of ordinary tobacco mosaic virus cause no obvious symptoms in tobacco (2). But, while it is true that some viruses multiply in some plants without causing symptoms by which a disease can be readily recognized, it is doubtful whether there are any really symptomless carriers. All viruses that become systemic and multiply within a plant probably cause some injury. However, the injury may be slight and easily overlooked unless control plants are available for comparison. Some virologists have gone so far as to suggest that there may be viruses capable of stimulating rate of growth in plants, but if such viruses exist they have not been discovered.

From viruses that cause exceedingly mild diseases, it is possible to pass by gradual steps to viruses that are lethal. We may, in fact, do this without going outside of the tobacco mosaic virus group. When masked strains of tobacco mosaic virus are propagated in tobacco, they are sooner or later replaced by mild mottling strains some of which approach ordinary tobacco mosaic virus in severity. Similarly, when severe strains are propagated in tobacco, they are replaced by milder strains some of which approach tobacco mosaic virus in mildness. All except the so-called masked virus strains cause marked stunting and other symptoms of disease. The masked virus strains cause stunting but no other well marked symptoms. Thus, the tobacco mosaic viruses and all other plant viruses may be classified as growth-depressing entities. This, however, does not mean that they depress rate of growth in all tissues.

The Fiji disease virus of sugarcane causes well marked galls in phloem tissues (4). The cranberry false blossom virus, with which the writer has

* Read at the 75th Anniversary Celebration of the Torrey Botanical Club at the Boyce Thompson Institute for Plant Research, Inc., Wednesday, June 24, 1942.

TORREYA for December (Vol. 43, 87–183) was issued February 10, 1944.

been working recently, causes increased growth in flowers. It depresses growth in the plant as a whole but stimulates rate of growth in flowers. In a number of different plants to which it has been taken, it causes the production of giant blossoms. Its action on tomato flowers is shown in figure 1. In the truss on the left the flowers are normal, while in the other two they are diseased. The sepals of the diseased flowers are much larger than sepals of normal flowers. Instead of remaining separate as in healthy blossoms, the affected sepals have fused to form a sac-shaped structure. When the sac was torn open, it was found that the petals were green in color and borne at the end of a thick stalk which was about an inch in length. The petals were leaf-like in structure; some

Fig. 1. False blossom in tomato. The flowering truss at the left is healthy; the other two are diseased. (Photograph by J. A. Carlile.)

were simple and others compound. The anthers were usually small and green. In its effects on tomato flowers, false blossom resembles the big-bud disease which occurs in the western part of this country (1) and in Australia (11). Other effects of false blossom on flower trusses are shown in figures 2 and 3. The diseased truss pictured in figure 2 was about four times as long as the healthy truss. It terminated in two stem tips bearing leaves. The stem of the diseased truss also was thicker than that of the healthy truss. Figure 3 shows other variations in the deformation of enlarged flower trusses.

Some diseased trusses that had not elongated so much but were borne on thick stems are displayed in figure 4 beside a normal truss. This type of malformation was met with less often than the big-bud type. Apparently there are several different strains of false blossom virus prevalent in nature. From some diseased cranberry plants a strain was obtained that caused a severe check to longitudinal growth but stimulated transverse growth. Plants with this strain stopped producing flower buds soon after they were infected and did not stimulate the production of secondary shoots. From other false blossom cranberry

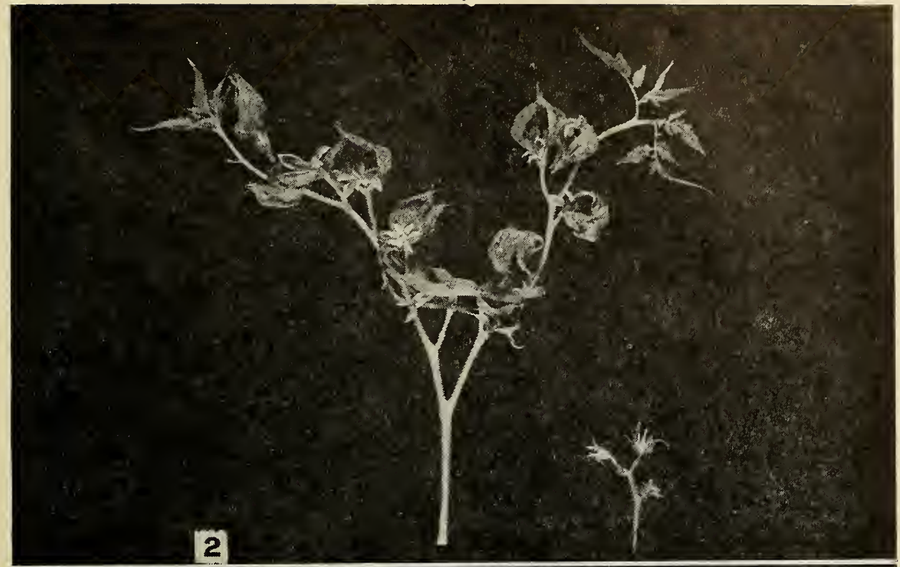

FIG. 2. False blossom in tomato. The flowering truss at the right is healthy; that at the left diseased. The picture shows the stimulating effect of the virus on flowering branches.

FIG. 3. False blossom in tomato. The three flowering trusses show different effects of the virus. (Photographs by J. A. Carlile.)

Fig. 4. False blossom in tomato. The flowering truss at the left is healthy; the other three are diseased, showing thickening of stems.

Fig. 5. False blossom in tomato. In the tip at the left longitudinal growth has been stimulated and transverse growth checked, while in the tip at the right longitudinal growth has been checked and transverse growth stimulated. The other three tips show intermediate effects. (Photographs by J. A. Carlile.)

plants a strain was obtained that stimulated longitudinal growth and checked transverse growth. This caused a spindling witches' broom type of growth. In tomatoes with the spindling strain no flower buds were produced except shortly after infection. The flowers that were produced usually were not more than two to three times the size of normal flowers. Between these extremes in which longitudinal growth was almost entirely stopped but transverse growth stimulated, on the one hand, and in which longitudinal growth was greatly stimulated but transverse growth severely checked, on the other hand, were strains that caused intermediate effects. Some of these are shown in figure 5 where tips from five different diseased tomato plants are pictured. The tip at the extreme right is greatly shortened and thickened; that on the extreme left is tall and spindly. The three types shown between these exhibited intermediate effects. The virus obtained from most diseased cranberry plants caused the symptoms shown by the tip in the center of the picture. This is the typical big-bud type of top where flowers are large and malformed and where considerable numbers of secondary shoots are produced. When scions from plants affected in this way and scions from plants showing the two extreme effects were grafted to healthy tomato plants, each came down with the type of disease characteristic of that shown by the plant from which the scion was taken. When the two extreme types were transmitted to periwinkle plants, they caused similar variations in symptoms. The virus that depressed longitudinal growth but stimulated transverse growth in the tomato caused the production of short thick tips but very little chlorosis or stunting of leaves when taken to periwinkles. The virus that stimulated longitudinal growth but depressed transverse growth in stems of the tomato produced similar effects in stems of periwinkles. In leaves it caused a marked chlorosis and narrowing. When the virus causing typical big-bud in tomato was taken to periwinkle, it caused the production of green malformed flowers such as are shown beside normal flowers in figure 6. When scions from periwinkles showing the different types of effects were grafted to healthy periwinkles, each transmitted the disease characteristic of the plant from which it was taken. While it has not been proved that these different types of disorders are caused by strains of the cranberry false blossom virus, this seems likely. When the common type of false blossom virus was transmitted to the composite, *Calendula,* it caused the production of malformed green flowers such as are pictured in figure 7 beside a healthy flower. Another plant in which false blossom virus caused gigantism in flowers was *Nicotiana glutinosa.* An early stage in the development of giant sepals is shown in figure 8, a late stage in figure 9. The blossoms at the left in both figures are normal; the others are diseased. Malformed leafy structures are shown protruding from some of the diseased flowers in figure 9. At the same time that the virus caused enlargement of flowers, it produced dwarfing of leaves.

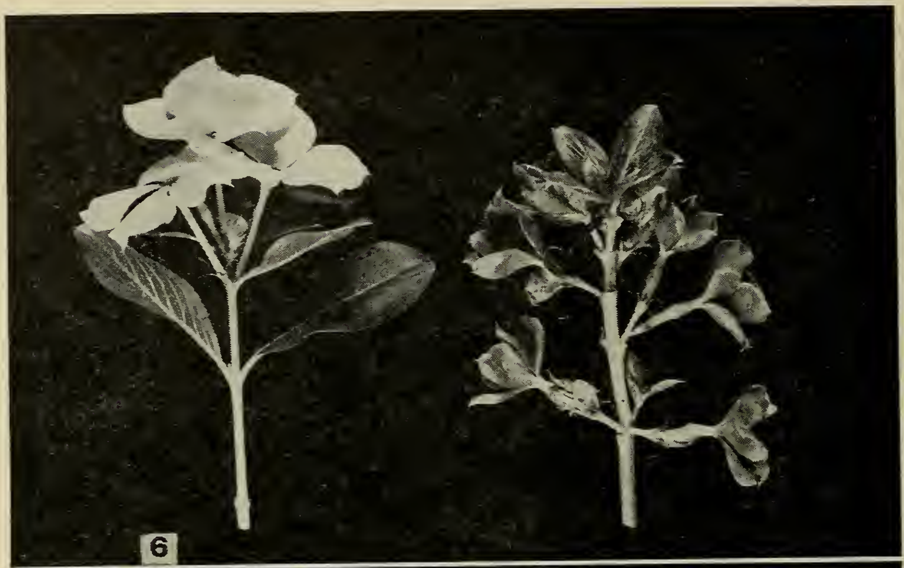

Fig. 6. False blossom in *Vinca rosea*. The flowering branch at the left is healthy; that at the right is diseased. The diseased flowers are malformed and virescent.

Fig. 7. False blossom in *Calendula*. The flower at the left is healthy; the other two are diseased. Affected flowers are green in color. (Photographs by J. A. Carlile.)

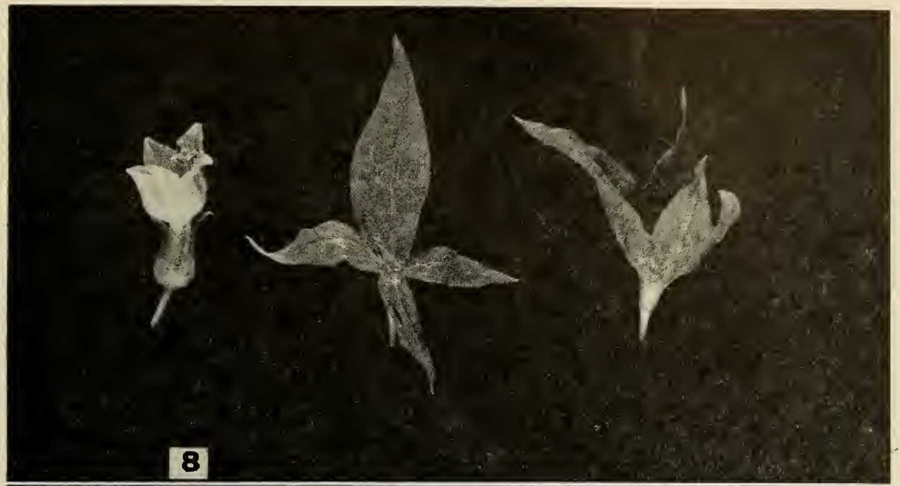

FIG. 8. False blossom in *Nicotiana glutinosa*. The flower at the left is healthy. The other two flowers have false blossom.

FIG. 9. False blossom in *Nicotiana glutinosa*. The flowering branch at the left is healthy; that at the right diseased, showing gigantism in flowers affected by the virus. (Photographs by J. A. Carlile.)

It would be possible to proceed at great length with the story of how false blossom virus upsets growth relationships, enlarges, distorts, and malforms flowers, and transforms plants of different species to such an extent that they can scarcely be recognized. But there would be no point in doing this, for the variability in the symptoms produced in different species is almost endless. It perhaps is sufficient to say that in all plants to which false blossom virus was taken it caused virescence and gigantism in flowers or parts of flowers, chlorosis and dwarfing in leaves, and an elongating or a shortening of internodes of stems.

Another effect of certain viruses on growth in plants that needs to be mentioned is repression of dormancy and maturity. Many biennial and perennial plants pass the winter in a dormant state. When brought into a greenhouse where good growing conditions are maintained and where they might be expected to grow continuously, they become dormant or semi-dormant as the winter season approaches. Many annual plants grow to maturity in a few months and then die. When affected by certain virus diseases, perennial plants fail to go into a dormant state regardless of environmental conditions. Peach trees affected by yellows disease do not stop growing as cold weather comes on but continue vegetative growth until the tender tips of branches are frozen and killed.

China aster plants set in the field late in May or early in June blossom in August and mature seeds in early autumn. By the time cold weather arrives, all healthy plants have died. The course of events is very different for plants that contract the aster yellows disease. They produce malformed virescent flowers and sterile seeds (5). It is true that some diseased plants produce viable seeds, but such seeds are borne only by flowers that have not been invaded by the virus. Instead of affected plants maturing and dying as cool weather approaches, they live and grow. They of course do not grow very fast and are eventually killed by low temperatures. But there is a period during which the only living plants in the field are those affected by the aster yellows disease. It is thus clear that the virus lengthens the life of the plant.

When healthy potato plants are grown in greenhouses, they produce tubers, mature, and die. If infected by the witches' broom virus, they produce tubers but they do not mature and die. Growth continues summer and winter for an indefinite period of time. There is a potted potato plant with witches' broom in one of our greenhouses that has been growing there for more than two years. Its healthy sister plants matured and died long ago. The witches' broom virus has had a favorable effect on the longevity of the plant.

Certain plant virus diseases are readily cured by heat. When affected plants are held at moderately high temperatures for appropriate periods of time, the viruses that cause these diseases are inactivated but the plants are not seriously injured. Peach yellows (6), aster yellows (7), and witches' broom of potato can be cured by heat in certain of the plants they affect. The false blossom disease also can be cured (8). When plants are cured, all of the bizarre effects produced by the viruses causing these diseases disappear. Cured peach trees become dormant when the season for dormancy arrives. Cured potato plants live no longer than healthy plants. The stimulating and stunting effects of cranberry false blossom virus in periwinkles subside and disappear when the plants are cured. It is apparent that these viruses affect growth only during the period in which they are present in the plants. The malformations that develop while plants are sick are of course not corrected by cure, but all new growth produced after plants are cured is normal. In this respect these viruses are like the growth-promoting substances. Their effects do not outlast the periods during which they are allowed to act but, unlike growth-promoting substances, viruses cause a retardation of growth in all plants in which they are permitted to multiply, although, as we have seen, they stimulate growth in certain tissues. They also are entirely unlike growth-promoting substances in that they infect, multiply, and cause disease.

Department of Animal and Plant Pathology
The Rockefeller Institute for Medical Research
Princeton, New Jersey

Literature Cited

1. Dana, B. F. Occurrence of big bud of tomato in the Pacific Northwest. Phytopath. **30**: 866-869. 1940.
2. Holmes, F. O. A masked strain of tobacco-mosaic virus. Phytopath. **24**: 845-873. 1934.
3. Jones, L. K., Anderson, E. J. & Burnett, G. The latent virus of potatoes. Phytopath. Zeitschr. **7**: 93-115. 1934.
4. Kunkel, L. O. Histological and cytological studies of the Fiji disease of sugar cane. Hawaiian Sugar Planters' Assoc., Exp. Bull., Bot. Ser., **3**: 99-107. 1924.
5. Kunkel, L. O. Sterility caused by the aster yellows disease. Mem. Hort. Soc. N. Y. **3**: 243-244. 1927.
6. Kunkel, L. O. Heat treatments for the cure of yellows and other virus diseases of peach. Phytopath. **26**: 809-830. 1936.
7. Kunkel, L. O. Heat cure of aster yellows in periwinkles. Am. Jour. Bot. **28**: 761-769. 1941.
8. Kunkel, L. O. False blossom in periwinkles and its cure by heat. Science **95**: 252. 1942.
9. McWhorter, F. P. A latent virus of lily. Science **86**: 179. 1937.
10. Nishimura, M. A carrier of the mosaic disease. Bull. Torrey Club **45**: 219-233. 1918.
11. Samuel, G., Bald, J. G. & Eardley, C. M. "Big bud," a virus disease of the tomato. Phytopath. **23**: 641-653. 1933.